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A NEW GYMNARTHRID MICROSAUR FROM THE LOWER PERMIAN OF KANSAS WITH A REVIEW OF THE TUDITANOMORPH MICROSAURS (AMPHIBIA)

By

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INTRODUCTION

Microsaurs are Paleozoic amphibians which have previously been included with Aïstopoda and Nectridia in one taxonomic unit, the Lepospondyli. The reason for this grouping was the presumed absence of intercentra in all members of the Lepospondyli. However, it has been shown (see Panchen, 1977: 310) that some microsaurs possess intercentra, and thus are not "lepospondylous." The microsaurs are therefore only distantly related to Nectridia and Aïstopoda. Carroll and Gaskill (1978) described all members of the order Microsauria. They divide the Microsauria into two suborders, the Microbrachomorpha and the Tuditanomorpha. Our paper is based primarily on their data and deals with the Tuditanomorpha. We assign a newly discovered Lower Permian microsaur to the Gymnarthridae within the suborder.

Six genera of microsaurs are assigned to the family Gymnarthridae (Carroll and Gaskill, 1978). This family ranges stratigraphically from the Lower Pennsylvanian (Joggins Formation, Westphalian B in Nova Scotia) to the Lower Permian (Hennessy Formation of Central Oklahoma, Clear Fork Formation of Texas). All described genera of Gymnarthridae are known from North America with one exception, *Sparodus*. *Sparodus* has been found in the Nýřany coal beds, Westphalia, Upper Carboniferous of Czechoslovakia. Four

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other genera, *Saxonerpeton, Trachystegos, Micraroter,* and *Rhynchonkos* will be discussed in their relation to the Gymnarthridae. Carroll and Gaskill (1978) assign *Saxonerpeton* to the Hapsidopareiontidae, *Trachystegos* to the Pantylidae, and *Micraroter* to the Ostodolepidae as does Daly (1973). *Rhynchonkos* (*Goniorhynchus* Olson, 1970)[2] is the only genus within the family Goniorhynchidae.

The terminology of skull bones of Carroll and Gaskill (1978) has been adopted throughout this paper. Evaluation of characters follows the method suggested by Hennig (1966), but the scheme is not transcribed into a rigid classification.

The new specimen described in this paper was found by B. Foreman in 1976 in the Lower Speiser Shale, Lower Permian, at Eskridge, Wabaunsee County, Kansas. The locality contained numerous remains of aquatic vertebrates, as follows:

Dipnoi: *Gnathorhiza* sp.
Amphibia:

Temnospondyli: *Acroplous vorax* Hotton, 1959
Nectridea: cf. *Diplocaulus*
Lysorophidea: *Lysorophus tricarinatus*

Lysorophus is the most common fossil in the locality; a nectridean (cf. *Diplocaulus*) and *Gnathorhiza* were also abundant. About fifteen specimens of the least common of the listed species, *Acroplous,* have been collected to date. All these aquatic vertebrates are well articulated in contrast to the fragmentary preservation of the associated terrestrial vertebrates which include a few fragmentary remains of reptiles and seymouriamorphs, and the skull of *Euryodus bonneri* n. sp. and one vertebral column of a microsaur. Continuous collecting has revealed no invertebrates or plants in association with the vertebrates. The fossils were found in a lenticular deposit of greyish-green mudstone variegated with red shale.

The new microsaur was prepared using Airbrasive and needle by O. Bonner and both authors. The final drawings were prepared by D. Bennett; the photographs were taken by J. Chorn. We appreciate the help of O. Bonner, D. Bennett, and J. Chorn, University of Kansas, Museum of Natural History, Lawrence, Kansas. We thank Dr. J. Bolt, Field Museum Chicago, and Dr. E. Daly, Museum of Natural History, Lawrence, for reading and commenting on the manuscript.

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[2] The generic name *Goniorhynchus* Olson 1970 is preoccupied by *Goniorhynchus* Hampson 1896, a Southeast and East Asian butterfly. We suggest replacing *Goniorhynchus* Olson 1970 by *Rhynchonkos,* a new name which expresses the same characteristics as Olson's name (ρύγχος gr. = snout, ονκοσ gr. = angle, hook).

DESCRIPTION

Class Amphibia
Order Microsauria Dawson 1863
Suborder Tuditanomorpha Carroll and Gaskill 1978
Family Gymnarthridae Case 1910
Genus *Euryodus* Olson 1939
Species *Euryodus bonneri* n. sp.

Diagnosis:—Small gymnarthrid microsaur with narrow skull. Posterior margin of the cheek region probably straight. The posterior border of the skull table straight to slightly undulated. The medial suture of the tabular forms a convex arch into the postparietal on the occiput. The prefrontal occupies a larger portion of the posterior margin of the external naris than the lacrimal. Lacrimal with a low dorsal process on the anterior margin of the orbit. Very large external nares, length about half of the length of the orbit. Pointed peg-like teeth.

Holotype:—KU VP 47367, a nearly complete, articulated skull with left lower jaw in place, but the right displaced below the skull; a few vertebrae and a humerus associated.

Horizon and locality:—Lower part of Speiser Shale, Council Grove Group, Lower Permian. Roadcut on Kansas State Highway 99, 1.5 miles northwest of Eskridge, Wabaunsee County, Kansas.

Derivatio nominis:—Named after Orville Bonner, Museum of Natural History, Lawrence, Kansas, who carefully prepared the specimen.

Description: Euryodus bonneri is represented by a single, nearly complete, articulated skull with the left lower jaw in natural position. All bones of the skull have a smooth surface, but a few grooves are developed in the snout region, on the rostral part of the lower jaw, and on the jugal. The pineal foramen is absent, but a low elevation is developed in that region.

The skull roof (Fig. 1A, 2B,C) shows all bones in their natural relation despite some crushing of the left side of the skull. The right cheek is not preserved. The middle portion of the right postparietal is vaulted upwards, and the lateral portion is pressed downwards anterolaterally. The posterior part of the right postparietal has been broken, and displaced downward and posteriorly. The postparietals are well developed onto the occiput. In dorsal view, the border of the occiput is nearly straight with a little undulation. The length of the postparietal (portion on the occiput + portion on the skull table) is ¾ of the length of the parietal (Table 1). The parietal and the frontal are of equal length, while the nasal is 80% of the length of the frontal or the parietal. The nasal forms the dorsal border of the external nares. Only the lateral
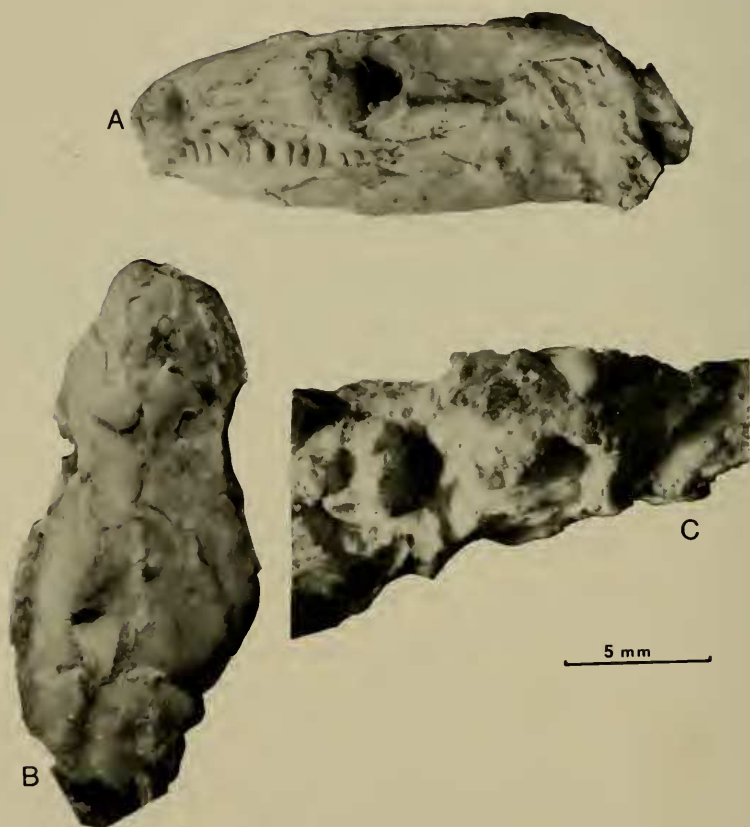
FIGURE 1.—*Euryodus bonneri* n. sp. (A) Skull in lateral view. *ca.* x 4.
(B) Skull in dorsal view. *ca.* x 4. (C) Vertebra. *ca.* x 4.

TABLE 1. Skull measurements in mm (l = left, r = right)

	length	width
skull	about 19	about 9
external naris	2.2	1.8
antorbital region	6.6	
orbit	4.4	3.1
postorbital region	7	
nasal	l 4.5	l 1.6
frontals	l 5.4/r 5.7	l 1.6/r 1.8
parietals	l 5.2/r 5.6	l 2.6/r 3.0
postparietal	l 4.2	l 2.3

part of the right nasal is preserved so that the rostral part of the right frontal which is normally overlapped by the nasal, is free. Frontals and nasals have equal width. The parietals are widest at the point where the suture between postfrontal and tabular meets the parietal. The parietals extend at this point as far laterally as the postparietals at the posterior border of the skull table.

Only the left tabular is preserved, and it is broken and pushed slightly over the postparietal and parietal towards the midline. The tabular extends onto the surface of the occiput contacting the postparietal along ⅔ of its venterocaudal extension; this means it does not reach venterocaudally to the same extent as the postparietal. The third dermal bone reaching onto the occiput, the squamosal, is missing. The postfrontal is a long bone, as long as parietal or frontal. The right postfrontal sends an anterior extension between prefrontal and frontal. Postfrontal and prefrontal each form about half of the dorsal margin of the orbit. The prefrontal is as long as the frontal. It extends from the dorsolateral margin of the orbit to the external naris. The anterior half of the prefrontal is expanded dorsoventrally. The prefrontal forms between ⅓ and ½ of the posterior margin of the external naris, it occupies more of the posterior margin than the lacrimal.

The lacrimal (Fig. 1B, 2A,D) extends from the external naris to the orbit. The ventral margin is broken, but nevertheless a dorsoventral widening in front of the orbit can be seen. The lacrimal forms most of the rostral border of the orbit. The opening for the nasolacrimal duct lies about in the middle of the anterior border of the orbit. It is not clear whether the lacrimal meets the rostral process of the jugal on the ventral margin of the orbit. The maxillary forms part of the floor of the orbit, and the maxillary possibly separates lacrimal and jugal on the ventral margin of the orbit.

The jugal (Fig. 1B, 2A,D) forms the lower margin of the orbit, and reaches half way up on the posterior margin. The rostral process is restored in Fig. 2D after the overlap area on the maxillary. From the posterior end of the maxillary on, the ventral margin of the jugal curves posterodorsally upwards to meet the posterior margin of the postorbital. The postorbital is smaller in size than the postfrontal. The dermal bones of the cheek region behind the jugal and the postorbital are not preserved, but there is a large space for a squamosal. As in other gymnarthrids, a quadratojugal may have formed the ventral margin of the cheek, perhaps reaching the maxillary under the posterior margin of the jugal. The posterior border of the cheek is vertical judging from a connecting line dropped from the border of the skull roof to the quadrate. The external nares of the specimen are very large and extend half the length of the orbit; their depth is ½ of their length and ⅗ of the

depth of the orbit (Table 1). The margin of the external naris is clearly visible, bordered by the bones or their impressions. The orbit is elongated, with the depth 70% of the length. The orbit is surrounded by the rim typical of microsaurs; the rim is well preserved on the lacrimal, jugal, and prefrontal, but is broken off on the other bones. The postorbital region is only slightly longer than the antorbital region. The antorbital length is divided in half by the posterior margin of the external naris.

The premaxillary (Fig. 1A, 2B,C) reaches the dorsal midline with a pointed process so that both premaxillaries together form a
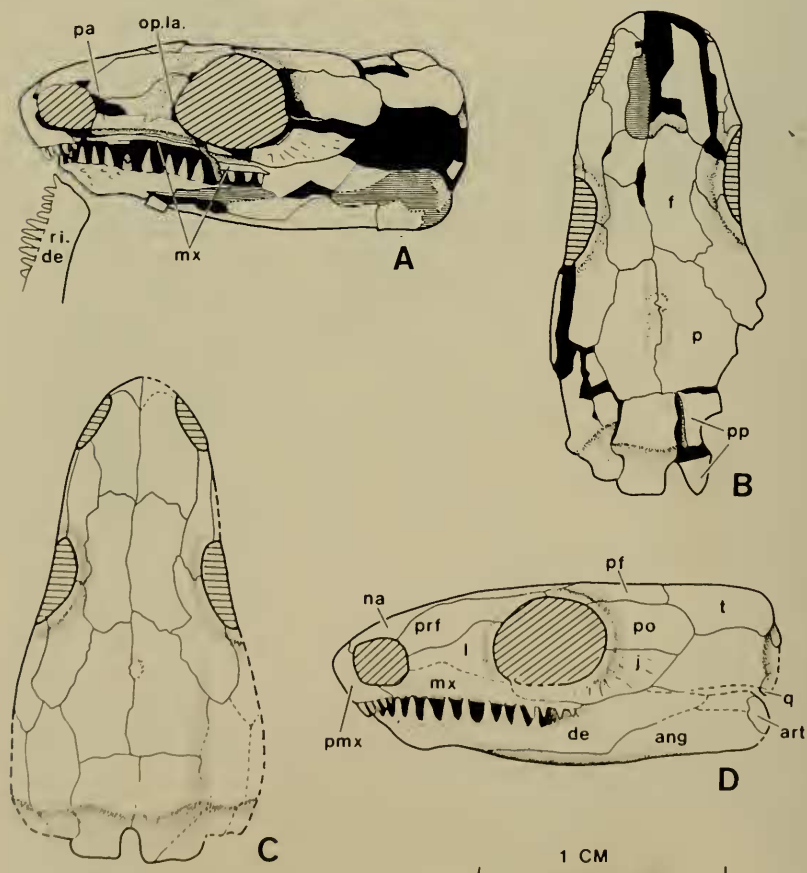
Figure 2.—*Euryodus bonneri* n. sp. (A,B) Skull unrestored: (A) in lateral view, (B) in dorsal view. (C,D) Restoration of the skull: (C) in dorsal view, (D) in lateral view.—*ang* angular, *art* articular, *de* dentary, *f* frontal, *j* jugal, *l* lacrimal, *mx* maxillary, *na* nasal, *op.la* opening of nasolacrimal duct, *p* parietal, *pa* palatine, *pf* postfrontal, *po* postorbital, *prf* prefrontal, *pp* postparietal, *q* quadrate, *ri.de* right dentary, *t* tabular; narrow horizontal hatching = impression.

triangle between the external nares. The premaxillary forms the rostral border and half of the ventral border of the external naris (Fig. 1B, 2A,D). It bears 5 teeth, with the front teeth being the largest, while only the base of the last small tooth is visible. The snout is prominent. Only the medial and the posterior portions of the left maxillary are preserved. The overlapping area of the jugal can be seen on the posterior portion of the maxillary, which bears four teeth, one larger anterior tooth only partially preserved and three smaller teeth behind diminishing in size posteriorly. The teeth are compressed mediolaterally. The lateral margin of the palatine is exposed between external naris and orbit where lacrimal and maxillary are absent. The palatine extends dorsally medial to the lacrimal and meets a process of the prefrontal extending ventrally on the anterior wall of the orbit.

The left lower jaw (Fig. 1B, 2A,D) is preserved in position, while the right is displaced with its axis inclining ventrally from the snout. The rostral and the posterodorsal part of the left dentary are preserved. The venterocaudal portion can be restored from the preserved impression and from the overlap area on the angular. The dentary bears only a low coronoid process. Eleven teeth can be counted on the exposed dorsal margin of the dentary, the full complement may be 12 or 13; the teeth are rounded at the base and more ovoid near the tip. The angular reaches far rostrally below the dentary, the suture between both bones is preserved posteriorly only as an impression. Only the ventral part of the angular is preserved, the boundaries to surangular and articular cannot be drawn with certainty. The angular does not extend onto the medial side of the lower jaw. It meets one bone (?prearticular) on the ventral margin of the lower jaw at the level of the posterior part of the tooth row. A piece of bone preserved on the posterior end of the lower jaw seems to be part of the articular. There is no sign of a retroarticular process.

Only little of the postcranial skeleton is associated with the skull: part of one humerus, and some vertebrae (Fig. 1C). The two pieces of the humerus are too fragmentary for comparison. The distal and the proximal ends are missing so that it is impossible to see if an entepicondylar foramen exists. One vertebra shows the deep posterior concavity, and the right side with the articulation area for the rib, and the zygapophysis with a flat articulating surface. The neural arch is missing. It is a typical microsaur vertebra, and the flat articulating surface is found in gymnarthrids. Near this vertebra, the ventral surface of the neural canal is exposed, on a piece longer than the first described vertebra.

COMPARISON AND DISCUSSION
Order Microsauria

Carroll and Gaskill (1978) include in the Microsauria those Paleozoic lepospondyl amphibians with squamosal and tabular but without supratemporal. In the Microsauria, the postparietal, tabular and squamosal reach with lappets onto the occiput, and there is no otic notch. A special articulation between the occipital condyle and the atlas is characteristic of these forms. The order Microsauria is divided into two suborders, the Tuditanomorpha and the Microbrachomorpha. The key differences in the skull roof between these suborders are:

1. The postfrontal is larger than the postorbital in early Tuditanomorpha, and subequal in size with the postorbital in later Tuditanomorpha, but smaller than the postorbital in Microbrachomorpha. This last feature is attained also in the most advanced Tuditanomorpha (*Pelodosotis*).

2. Postfrontal and postorbital are in contact with the tabular in Tuditanomorpha (exception: *Hapsidopareion*). In Microbrachomorpha, the parietal extends laterally to separate the postfrontal from the tabular.

3. Parietal, frontal, and nasal are subequal in size in Tuditanomorpha, but the parietal is wider than the frontal, and the frontal wider than the nasal in Microbrachomorpha.

In all these characters the described specimen compares with the Tuditanomorpha. Thus, we need to discuss the Tuditanomorpha only. The character states for the families of Tuditanomorpha will be evaluated by comparison with those of the Microbrachomorpha, the closest outgroup comparison possible. In addition, anthracosaurs (=Batrachosauria, see Panchen, 1970) are taken for comparison outside the microsaurs because they are considered here as the more primitive group most closely related to the microsaurs. The relation between tabular and parietal, the pleurocentrum presumably forming the main part of the vertebral centrum (see Panchen, 1977), occurrence of a supraoccipital (see Panchen, 1972) are in favor of a close relationship of microsaurs to anthracosaurs (see Gaffney, 1979: 99). "Apart from the skull characters discussed, only the atlas-axis complex significantly distinguishes microsaurs from the other two" (=anthracosaurs and early reptiles; Panchen, 1972: 85).

Suborder Tuditanomorpha

Carroll and Gaskill (1978) recognize seven families within the Tuditanomorpha. Following Carroll and Gaskill (1978) and our own judgment, we chose the characteristics of the families to get a testable scheme of the relationship of Tuditanomorpha so that

we could evaluate the significance of the characters in the new specimen. Figure 3 shows the interrelationships of six of the families within the Tuditanomorpha, excluding the Trihecatontidae. The following characters numbered 1 to 8 have been used as key characters of the families in Figure 3; character 0 is not distinctive enough to separate any family.

(0) *Size relation between postfrontal and postorbital:* Microsaurs are characterized by the absence of intertemporal and supratemporal. Tuditanomorpha and Microbrachomorpha follow different patterns in occupying the space of intertemporal and supratemporal. A lappet of the parietal occurs in place of the intertemporal and supratemporal in the Microbrachomorpha; the tabular and postfrontal expand into this space in the Tuditanomorpha.
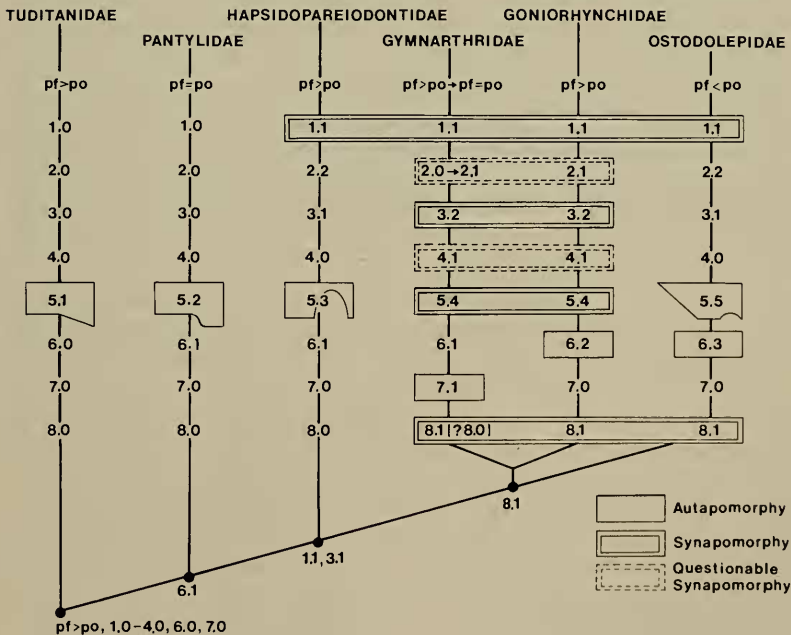
FIGURE 3.—Interrelationship of the families of the suborder Tuditanomorpha. *pf* postfrontal, *po* postorbital. (1) Position of the jaw articulation: (1.0) at the level and (1.1) in front of the occipital condyle-atlas articulation. (2) Posterior margin of the cheek region: (2.0) straight, (2.1) inclined backward, (2.2) inclined forward. (3) Quadratojugal: (3.1) large, (3.1) small, (3.2) elongated. (4) Epicondylar foramen: (4.0) present, (4.1) absent. (5) Margin of the upper jaw: (5.1) posterior margin inclined, (5.2) ventral extension, (5.3) deep emargination up to tabular, (5.4) straight, (5.5) low emargination. (6) Posterior margin of skull table: (6.0) concave, (6.1) straight, (6.2) convex, triangular, (6.3) undulated, emargination at the occiput. (7) Supraoccipital: (7.0) present, (7.1) absent. (8) Number of presacral vertebrae: (8.0) below 30, (8.1) 37 and more.

Thus, the postfrontal extends about as far posterior as does the postorbital in the Tuditanomorpha, whereas it is limited to the region close to the orbit in the Microbrachomorpha. The postfrontal is larger than the postorbital in primitive Tuditanomorpha, while the postfrontal is smaller than the postorbital in the Microbrachomorpha. In both groups, these bones tend to become the same size. The postorbital becomes larger than the postfrontal in the specialized tuditanomorph Ostodolepidae. The evolutionary tendency towards enlargement of the postorbital is quite evident within the Tuditanomorpha, but the character is too transitional to be used for characterizing any family.

(1) *Position of the jaw articulation:* The jaw articulation lies well behind the occiput in anthracosaurs, but on the level with or in front of the articulation between occiput and first vertebra in most microsaurs. Only some Tuditanidae (*Tuditanus,* Carroll and Gaskill, 1978, fig. 4) show the more primitive situation with the jaw articulation a little further posterior. All Pennsylvanian Tuditanomorpha and the Permian genera *Saxonerpeton* and *Pantylus* have both articulations on the same level. The anterior position of the jaw articulation is acquired in Hapsidopareiodontidae, Gymnarthridae, Goniorhynchidae, and Ostodolepidae and in parallel in the Microbrachomorpha. Within the Microbrachomorpha, only *Hyploplesion* has both articulations at the same level (Carroll and Gaskill, 1977, Fig. 89, E,H).

(2) *Posterior margin of the cheek region:* Microsaurs do not possess an otic notch so that the cheek has a straight posterior margin from the skull roof down to the jaw articulation. This margin is nearly straight vertically in most microsaurs as one may expect from the relation of the posterior end of the tabular to the quadrate in anthracosaurs, considered here as the primitive sister-group of microsaurs. The occiput (thus the posterior margin of the cheek) is inclined forward in burrowing forms. This feature is more pronounced in *Hapsidopareion* than in *Llistrofus* within the Hapsidopareiontidae, and extreme in *Pelodosotis* within the Ostodolepidae. In our opinion, this feature is an expression of burrowing adaptation rather than a synapomorphy; it occurs in the Ostodolepidae along with a subterminal mouth. The backward inclination of the margin of the cheek is a tendency within gymnarthrids and *Rhynchonkos*; thus, the margin is inclined forward in the largest gymnarthrid. The feature may or may not be a synapomorphy for *Rhynchonkos* and some gymnarthrids.

(3) *Quadratojugal:* The quadratojugal differs in size within microsaurs. It is large and relatively deep in all Microbrachomorpha except *Odonterpeton*, in Tuditanidae, and in Pantylidae. It is a large and relatively deep bone in anthracosaurs and most other Carboniferous amphibians. That seems to be the primitive situa-

tion. The quadratojugal becomes small in Tuditanomorpha and Microbrachomorpha (*Odonterpeton*), while a low elongated shape is found in gymnarthrids and goniorhynchids only; therefore, it seems to be an advanced feature for both families.

(4) *Entepicondylar foramen:* The entepicondylar foramen is present in microsaurs as in anthracosaurs. It has, therefore, to be considered as primitive for microsaurs, and the loss as advanced. It is lost within Microbrachomorpha and within Tuditanomorpha, and it may be lost independently more than once within each suborder. Most gymnarthrids and goniorhynchids have no entepicondylar foramen, although Carroll and Gaskill (1978) describe an isolated gymnarthrid humerus with an entepicondylar foramen. The shape of the humerus in gymnarthrids is different from other Tuditanomorpha, and resembles that of Goniorhynchidae (Carroll and Gaskill, 1978: 175).

(5) *Margin of the upper jaw:* The ventral margin of the upper jaw is a good character to distinguish the families within the Tuditanomorpha. It changes in the extremes from a ventral extension to a deep dorsal emargination. The slight ventral extension of the cheek region behind the toothed maxillary in Tuditanidae is the primitive situation judging from a similar situation in Microbrachomorpha (*Microbrachis* after Steen, 1938; or *Hyloplesion* after Carroll and Gaskill, 1978) and anthracosaurs (Panchen, 1970). The Pantylidae evolve a broad ventral lappet, while Hapsidopareiontidae and Ostodolepidae have an emargination instead. The emargination in both families is quite different, and very deep in Hapsidopareiontidae. Only Gymnarthridae and Goniorhynchidae seem to be comparable in the formation of the ventral margin of the cheek region: a straight margin with the tendency to be arched.

(6) *Posterior margin of skull table:* The primitive position of the jaw articulation is posterior to the occipital region. Consequently, the closing of the otic notch has imposed a concave shaped margin along the posterior edge of the skull table. In those forms in which the posterior margin of the skull table is straight, there is little difference in the configuration of the skull elements along the posterior margin when compared with the more primitive concave shape. The significant difference is the anterior placement of the quadrate in the forms with straight posterior skull table margin.

Only the forms considered to be best adapted for burrowing show a different limit for attachment of the neck musculature. Thus, in Ostodolepidae (and BPI 3839, see Carroll and Gaskill, 1978), the musculature extends anterior and lateral to the occipital articulation in such a way that the posterior margin of the skull roof forms an undulating line. The margin of the skull table lies relatively far forward in *Rhynchonkos*, which also results from the extreme posterior position of the occipital articulation. The pos-

terior margin of the skull table in *Rhynchonkos* forms a shallow posterior projecting triangle with the apex nearly reaching the supraoccipital.

(7) *Supraoccipital:* An ossified supraoccipital exists in anthracosaurs (Panchen, 1970), and it may be primitively present in all microsaurs even though it is not known in Microbrachomorpha. It is comparatively large in Tuditanidae, Pantylidae, and Hapsidopareiontidae. It is reduced in *Rhynchonkos* and in Ostodolepidae, and missing only in the Gymnarthridae. The latter advanced feature may be an autapomorphy for Gymnarthridae distinguishing them from *Rhynchonkos*.

(8) *Number of vertebrae:* A low number of trunk vertebrae (about 25) is "the normal count" (Panchen, 1970: 28) in labyrinthodonts, although the anthracosaur *Archeria* has more than forty. A count below 30 is found in most microsaurs. Only *Microbrachis* within the Microbrachomorpha, and the Gymnarthridae, *Rhynchonkos,* and to an extreme, the Ostodolepidae within the Tuditanomorpha exceed the number thirty. This feature is here considered an advanced feature within the Tuditanomorpha.

Within the microsaurs most of the above characters (1, 2, 3, 6, 7) evolve towards a reptilian state as has been observed earlier (see Carroll and Baird, 1968). These are useful characters to separate the families of Tuditanomorpha after one accepts the basic characters which unite the microsaurs into a monophyletic group not ancestral or closely related to reptiles. The genera of the Tuditanidae are the most primitive ones within the suborder; the shape of the occiput, the ornamentation of the bones, the size of the quadratojugal, and the high number of marginal teeth are all characters primitive within the suborder. The Pantylidae are only a little more advanced. The ventral extension of the margin of the upper jaw is the main character of the family. The number of teeth is reduced as in no other family of the suborder (3 premaxillary teeth, and 8-9 maxillary teeth, contrary to 5 premaxillary and more than 16 maxillary teeth in most Tuditanomorpha) except the Gymnarthridae where the number can drop to 10 maxillary teeth in advanced forms. In addition, the configuration of the suture pattern (interdigitating sutures), the ovoid shape of the eye, and the long postorbital length justify the family. The genera of Hapsidopareiontidae are distinguished from other Tuditanomorpha by the high emargination of the cheek up to the tabular. In Ostodolepidae, the emargination of the cheek region is not as high, and the skull is shaped quite differently. The Ostodolepidae are the most specialized forms within the Tuditanomorpha, the "extreme diggers" with pointed snout, triangular skull, and inclined occipital region. The last two families, the Goniorhynchidae and the Gymnarthridae (the Trihecatontidae are set aside because too little is

known about them), have many features in common (Fig. 3). Only the shape of the occiput seems to give the possibility of distinguishing clearly both families. The shape of the teeth and the number of teeth are characters considered to be of high value in separating both families for Carroll and Gaskill (1978: 155), but these are primitive characters (compare *Saxonerpeton* within the family). On the contrary, the existence of many advanced characters in both families could even be used to consider *Rhynchonkos* as one of the Gymnarthridae.

A character obliterated many times in parallel is the loss of the pineal opening. It is lost in Pantylidae, Ostodolepidae, some Gymnarthridae (*Pariotichus, Euryodus primus* and *E. bonneri*), and in "*Micraroter*" BPI 3839 (not in the type of *Micraroter*). The elongation of the trunk is a feature shown in Goniorhynchidae, Gymnarthridae, and Ostodolepidae. In these forms, the intercentrum is ossified also (these characters are known from the otherwise poorly known Trihecatontidae so that it can be argued at least that this family may have some relation to one of these families). Within the Gymnarthridae, *Euryodus* (*peabodyi, primus,* and *dalyae*) possesses strap-shaped intercentra. Vertebrae of other gymnarthrid genera are not known. The Pennsylvanian *Hylerpeton* shows some vertebrae formed by the pleurocentrum only so that Carroll and Gaskill (1978: 59) stated: "Their [intercentra] apparent absence in other forms could be attributed either to absence of ossification or postmortem disturbance. The apparent absence of intercentra in Pennsylvanian gymnarthrids . . . ." *Rhynchonkos,* the only genus within the Goniorhynchidae, shows small intercentra. The situation in Ostodolepidae, and in *Micraroter* is ambiguous. *Ostodolepis* itself has intercentra, but the other genus *Pelodosotis* within the family shows none. The type specimen of *Micraroter* has no intercentra, but intercentra are present in BPI 3839, a specimen assigned to the same genus by Carroll and Gaskill (1978). Therefore, presence or absence, and shape of intercentra cannot be used to characterize families within the Tuditanomorpha.

In conclusion, the six families within the Tuditanomorpha which can be defined by cranial characters are accepted by the authors. We disagree with the assignment of some genera to a particular family (see below). Gymnarthridae and Goniorhynchidea are the two most closely related families. The position of the seventh family, Trihecatontidae, is uncertain because of lack of data. The described specimen agrees in all its characters with the members of the Gymnarthridae.

Genera *Incertae Sedis*

Four genera within the Tuditanomorpha do not conform to the

characteristics of the families they are assigned to by Carroll and Gaskill (1978):

Saxonerpeton and *Ricnodon: Saxonerpeton* is assigned to the Hapsidopareiontidae although it lacks the emargination of the cheek region, the most characteristic feature of the family (Carroll and Gaskill, 1978: 38). The margin of the upper jaw is straight, and the quadratojugal is elongated as in Gymnarthridae and Goniorhynchidae. The maxillary reaches the orbit as in some Gymnarthridae, and in the type of *Micraroter*. The arrangement of the bones of the skull roof is similar to Gymnarthridae. The postparietals seem to take more space on the skull roof (Carroll and Gaskill, 1978, fig. 19A,B, 21) than in the given restoration (Fig. 22). The prefrontal reaches very far rostrad in Gymnarthridae, as in Hapsidopareiontidae. A dentary forming most of the external side of the lower jaw together with a reduced angular is likewise a feature of the Gymnarthridae. The interclavicle is similar to that in the Gymnarthridae. In conclusion, the authors prefer to place this genus close to the Gymnarthridae, even though there are some primitive characters as the low number of presacral vertebrae, the high number of teeth, and an entepicondylar foramen in the humerus of *Saxonerpeton* (but an entepicondylar foramen is present also in an isolated gymnarthrid humerus, see Carroll and Gaskill, 1978, Fig. 41B).

Carroll and Gaskill (1978) put *Ricnodon* very close to *Saxonerpeton,* but there is very little known which could give us their proper relationship. As in *Saxonerpeton,* the characteristic emargination of the cheek region of Hapsidopareiontidae is not known. The pelvic girdle, as in *Saxonerpeton,* is different from Hapsidopareiontidae and matches with that of *Rhynchonkos* and the Microbrachomorpha, and therefore we assume it is a primitive feature. Diagnostic features can be found in the lower jaw and the jugal only (Fritsch, 1883, Plate 42; or Carroll, 1966, Fig. 18). The surangular is very large; this is a primitive feature in Tuditanomorpha and found only in Tuditanidae. The ventral extension of the jugal indicates a ventral extension of the margin of the upper jaw, a diagnostic feature of Tuditanidae. If the specimens from Joggins are assigned correctly to *Ricnodon* (Carroll, 1966: 86-89), the two dorsal processes of the ilium, and the large pineal foramen agree with features in Tuditanidae. The position of *Ricnodon* is difficult to determine, but all known features would justify an assignment to the Tuditanidae; even here the existence of the entepicondylar foramen raises no problems.

Trachystegos: Very little is known of this genus. It is assigned to the Pantylidae (Carroll and Gaskill, 1978) even though the extension of the margin of the upper jaw (p. 11) has not been determined. The dermal bone pattern does not resemble that of

Pantylus either. The prefrontal reaches far forward, the lacrimal has a dorsal process at the anterior margin of the orbit, and the maxillary reaches the ventral margin of the orbit. All these are features of the Gymnarthridae, but an entepicondylar foramen is present. The fragments of *Trachystegos* do not provide enough evidence to include the genus within the Gymnarthridae with certainty (but see further discussion on p. 23).

Micraroter: Carroll and Gaskill (1978) assign two specimens to *M. erythrogeios*, the type specimen described by Daly (1973) and one specimen of the Bernard Price Institute of Paleontological Research, Johannesburg (BPI 3839). BPI 3839 possesses the emargination characteristic for Ostodolepidae, but the cheek is not preserved in the type specimen. In the type specimen, the prefrontal reaches the external naris, and the lacrimal has a high dorsal process at the anterior margin of the orbit. These are features of Gymnarthridae, and lacking in BPI 3839. It follows from these and other characters that BPI 3839 and the type of *Micraroter erythrogeios* do not belong to the same genus. The first may be closer to Ostodolepidae because of the main character cheek emargination, but the latter closer to the Goniorhynchidae/Gymnarthridae (Fig. 4 shows a reconstruction of the missing cheek region with a broader anterodorsal portion of the squamosal as found in Gymnarthridae and Goniorhynchidae; there is not much space left for an emargination). In addition, the cervical vertebrae of the type specimen of *Micraroter* show similarities in the shape of the neural arch with Gymnarthridae (compare Carroll and Gaskill, 1978, Fig. 115F with 115E and C); the neural arches of BPI 3839 (Fig. 115G) are quite different. On the other hand, BPI 3839 possesses intercentra similar (Fig. 59A, but in contrast to the reconstruction in Fig. 60C) to those in *Euryodus*, but the type specimen of *Micraroter* does not show intercentra. Even though *Micraroter erythrogeios* and BPI 3839 belong to different genera, they show that the Ostodolepidae are more closely related to Goniorhynchidae and Gymnarthridae than to any other Tuditanomorpha.

Family Gymnarthridae

The Gymnarthridae are the family with the highest number of genera and species within the Tuditanomorpha, and the new form belongs in this family (see above). Carroll and Gaskill (1978) often use size to assign specimens to genera. This seems to be a weak argument. Because of insufficient knowledge of many gymnarthrids Carroll and Gaskill (1978: 76) state that "the possible interrelationship of the various genera is open to speculation." Contrary to Carroll and Gaskill (1978), let us speculate on the use of defined characters in the hope of attaining the means to assign the described specimen to the proper genus. A series of characters
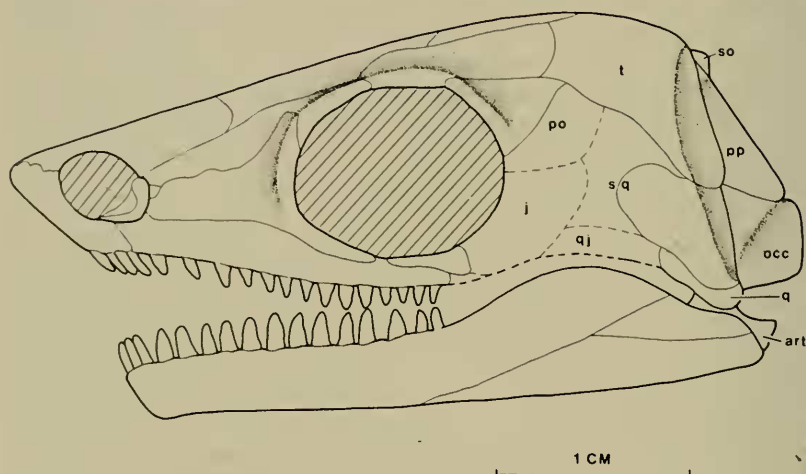
FIGURE 4.—*Micraroter erythrogeios* Daly, skull in lateral view (after Carroll and Gaskill, 1978, Fig. 53; changed in the missing cheek region).—*art* articular, *j* jugal, *occ* occipital, *po* postorbital, *pp* postparietal, *q* quadrate, *qj* quadrato-jugal, *so* supraoccipital, *sq* squamosum, *t* tabular.

has been used to define the different genera and species within the Gymnarthidae and their relationship (Fig. 6):

(1) *Prefrontal:* The prefrontal occupies a similar space as in anthracosaurs; it reaches far forward but does not reach the external naris. The later advanced condition is acquired in the new species and in *E. dalyae, E. peabodyi*, and in some specimens of *E. primus.*

(2) *Position of the jaw articulation:* It has been shown above (p. —) that the jaw articulation is situated at the level of the occipital articulation in primitive Tuditanomorpha. In Gymnarthridae, the jaw articulation is always in front of the occipital articulation, and it moves even farther anterior in more advanced species like *Cardiocephalus sternbergi.*

(3) *Size of orbit:* The orbit is usually larger in juvenile specimens than in adults, so this criterion is often used as an indication of juvenility. Small specimens often have a larger orbit (compared to the length of the skull) than larger specimens. We find within the Tuditanomorpha that the members of the more primitive families have very large orbits even when the specimens are large (i.e., *Crinodon*). There seems to be a tendency in more advanced Tuditanomorpha towards smaller orbits. The largest orbit (length of orbit to length of skull) of specimens figured in this paper can be found in the smallest (*Saxonerpeton*, Fig. 5A) and in the largest (*Micraroter*, Fig. 4) forms. This demonstrates that there is not only a tendency towards smaller orbits, but another tendency to keep large eyes. The gymnarthrids generally have smaller orbits with a

length below 20 percent of the skull length with the exception of
E. bonneri (Fig. 5E).

(4) *Size of external nares:* The size of the external nares is re-
lated to the size of the specimens; it is relatively large in small
specimens. Thus, the external nares are proportionately larger in
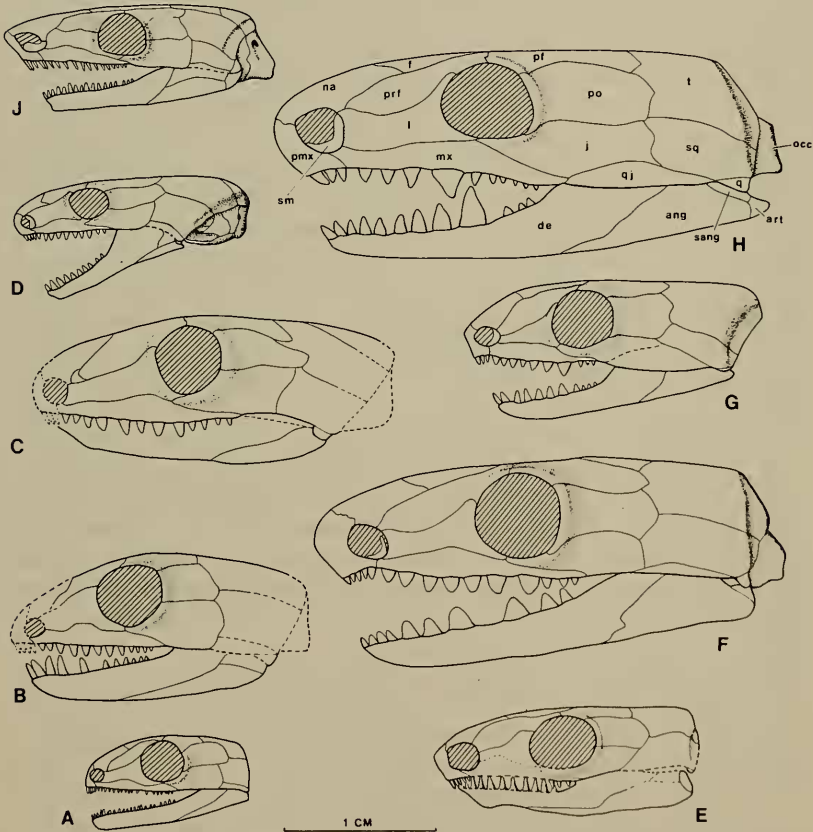
FIGURE 5.—Skulls in lateral view of Gymnarthridae and Goniorhynchidae
(after Carroll and Gaskill, 1978; changed); all x 2. (A) *Saxonerpeton geinitzi*
(Credner) (*ibid.,* restoration Fig. 22 changed after Fig. 21); (B) *Leioce-
phalikon problematicum* (Dawson) (*ibid.,* restoration Fig. 46C); (C)
Pariotichus brachyops Cope (*ibid.,* restoration Fig. 45C changed after Fig.
45A); (D) *Cardiocephalus sternbergi* Broili (*ibid.,* restoration Fig. 30C
changed after Fig. 30A); (E) *Euryodus bonneri* n. sp.; (F) *Euryodus dalyae*
Carroll and Gaskill (*ibid.,* restoration Fig. 43 changed after Fig. 42A); (G)
Euryodus peabodyi (Carroll and Gaskill) (*ibid.,* restoration Fig. 32 changed
after Fig. 32 and KU VP 8967); (H) *Euryodus primus* Olson (*ibid.,* restoration
Fig. 37 changed after Figs. 36 + 38A); (J) *Rhynchonkos stovalli* (Olson)
(*ibid.,* restoration Fig. 64).—*ang* angular, *art* articular, *de* dentary, *f* frontal,
j jugal, *l* lacrimal, *mx* maxillary, *na* nasal, *occ* occipital, *pf* postfrontal, *pmx*
premaxillary, *po* postorbital, *prf* prefrontal, *q* quadrate, *qj* quadratojugal, *sang*
surangular, *sm* septomaxillary, *sq* squamosum, *t* tabular.

microsaurs than in the larger anthracosaurs. There is the tendency towards smaller external nares (compared to the length of the skull). In *E. bonneri*, the external nares are even more enlarged, while *C. sternbergi* shows the tendency towards smaller external nares as in other Tuditanomorpha.

(5,6,13) *Number of teeth on premaxillary, on maxillary, and on the margin of the lower jaw:* The number of teeth is high in primitive Tuditanomorpha as in Microbrachomorpha. The number of teeth on all three bones is reduced in all families of Tuditanomorpha compared to the Tuditanidae. Seven premaxillary teeth interpreted as the primitive state occur in some members of the Tuditanidae and Microbrachomorpha. In the more advanced tuditanomorph families the number is reduced to five; in the Pantylidae to three. The later reduced number also occurs in two species of Gymnarthridae (*E. peabodyi* and *E. primus*), a synapomorphy of these two species and a convergence in Pantylidae assumed after the phylogenetic position of both groups. Gymnarthridae have fewer marginal teeth on the maxillary and the lower jaw. Only the Pantylidae have less teeth on the lower jaw than the Gymnarthridae.

(7) *Number of small teeth behind enlarged teeth on the maxillary:* A differentiation between premaxillary teeth ("incisors") and maxillary teeth occur in *Pantylus* and Gymnarthridae. In *Pantylus* the first maxillary tooth is enlarged ("canine"), while all maxillary teeth are enlarged in Gymnarthridae except the most posterior ones. The enlargement of maxillary teeth includes progressively more posterior teeth so that fewer and fewer small teeth are found in the posterior part of the maxillary.

(8) *Retroarticular process:* A retroarticular process is found only in the largest representative within the Gymnarthridae.

(9) *Shape of lacrimal at the anterior margin of the orbit:* The lacrimal extends from the external naris to the orbit in all microsaurs. It has a ventral extension along the margin of the orbit, and it meets the rostral extension of the jugal. That is the shape of the lacrimal found in nearly all microsaurs, but the lacrimal extends dorsally along the anterior margin of the orbit in some forms (*Crinodon* within the Tuditanidae; *Pariotichus, Euryodus,* and *Cardiocephalus* within the Gymnarthridae; *Pelodosotis* within the Ostodolepidae; and the holotype of *Micraroter*). This shape is acquired in parallel in these families because their more primitive members lack this feature. The shape is very similar to the shape of the lacrimal in captorhinomorphs, another parallel evolution. The ventral extension may be reduced in *Cardiocephalus sternbergi*.

(10) *Quadratojugal:* The elongated, narrow shape of the quadratojugal is one of the advanced characters of the Gymnarthridae and Goniorhynchidae (Fig. 3). The quadratojugal is primi-

tively situated between the jugal and the quadrate. It extends rostrad below the jugal in some gymnarthrids, and it reaches the maxillary in *E. primus* and possibly in *E. peabodyi* also.

(11) *Posterior margin of the skull table:* In dorsal view straight posterior margin of the skull table is the common feature of gymnarthrids above Tuditanidae (Fig. 3). The margin becomes convex with the backward inclination of the posterior margin of the cheek region in *Cardiocephalus sternbergi,* and to some extent in *E. peabodyi. E. primus* shows a tendency towards this feature (Carroll and Gaskill, 1978, Fig. 36-38).

(12) *Posterior margin of the cheek region:* A vertical posterior margin of the cheek region is primitive within Tuditanomorpha (Fig. 3). Burrowing forms tend to have a forward-inclined posterior margin of the cheek region. That seems to be the tendency in one gymnarthrid species, *E. primus* (after the restoration by Carroll and Gaskill, 1978, Fig. 37), but otherwise gymnarthrids tend to have a backward-inclined posterior margin of the cheek, with the most extreme example being *Cardiocephalus sternbergi.*

Only the Permian gymnarthrid genera are sufficiently known to evaluate their interrelationships. Three genera, *Cardiocephalus, Euryodus,* and *Pariotichus,* are known from the Permian of Texas, Oklahoma and Kansas. Carroll and Gaskill (1978) placed *C.* cf. *sternbergi* as *E. dalyae* into the genus *Euryodus* because of difference in size with both genera, *Euryodus* and *Cardiocephalus,* containing two species. There exist more differences between the two genera than simply size (Figs. 5, 6). *Cardiocephalus* (Fig. 5D) has a long, low skull with a large postorbital length, and the jaw articulation lies far rostrad from the occipital condyle-atlas articulation (distance nearly 25% of skull length) as compared with other gymnarthrids. The posterior margin of the cheek is strongly inclined backwards comparable to the situation in *Rhynchonkos* (Fig. 5J). The external naris is the smallest within the gymnarthrids. The lower jaw possesses a high coronoid process.

In contrast to *Cardiocephalus, Euryodus* (Fig. 5F,H) shows a short distance between the occipital condyle-atlas articulation and the jaw articulation (about 12% of skull length). The occiput is nearly straight or slightly inclined posteriorly. The external naris is large even in proportion to the large orbit (up to 50% of orbit length). The teeth are enlarged, and one prominent feature which caused us difficulties at first is the long prefrontal reaching the external naris, a feature found in nearly all specimens of *Euryodus* and in the type specimen of *Micraroter* (but not in BPI 3839). The lacrimal exhibits a process dorsally on the anterior margin of the orbit as in *Pariotichus,* and the quadratojugal is prolonged rostrad so that it meets the maxillary in the type species of the genus. If we apply these characters on the four species assigned by Carroll

SAXONERPETON   PARIOTICHUS   EURYODUS   CARDIOCEPHALUS

LEIOCEPHALIKON   bonneri   dalyae   peabodyi   primus   sternbergi

pf =po   pf > po   pf = po   pf=po   pf=po   pf=po   pf =po   pf > po

| | |
1.1   1.1   1.1   1.2   1.2   1.2   1.1-1.2   1.0
| | |
2.0   2.0   ?   2.1   2.1   2.1   2.1   2.2
| | |
3.0   3.1   3.2   3.1   3.2   3.2   3.2   3.2
| | |
4.0   4.2   ?   4.1   4.0   4.0   4.0   4.2
| | |
5.5   ?   ?   5.5   5.5   5.3   5.3   5.4
| | |
6.22   6,12   6,12   ?   6.10   6.10   6.10   6.10
| | |
7.0   7.1   7.1   7.2   7.2   7.2   7.21   7.3
| | |
8.0   8.0   8.0   8.0   8.0   8.0   8.1   8.0
| | |
9.0   9.0   9.1   9.1   9.1   9.11   9.11   9.2
| | |
10.0   10.0   ?   10.1   10.1   10.1-10.2 10.2   10.0
| | |
11.0   ?   ?   11.0   11.0   11.1   11.0   11.1
| | |
12.0   ?   ?   12.0   12.0   12.1   12.2   12.11
| | |
13.22   13.12   ?   13.12   13.10   13.12   13.12   13.10
?   ?
| |

Autapomorphy

Synapomorphy

Questionable
Synapomorphy

6.10, 7.2, 11.0

9.1

6.12, 7.1, 13.12
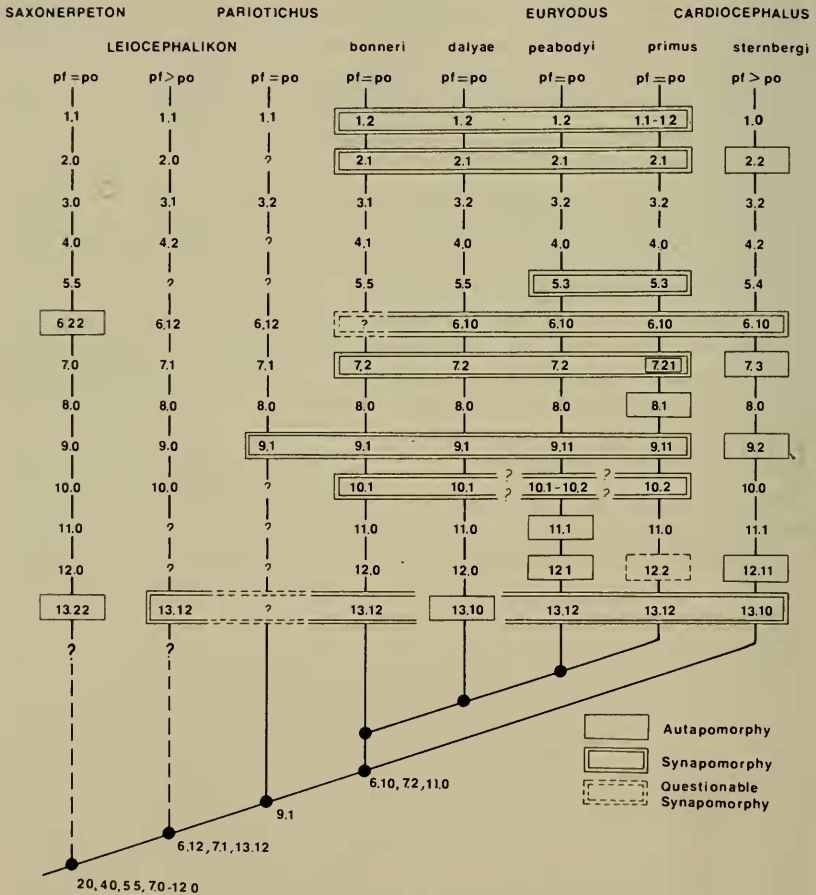
20, 40, 5.5, 7.0-12.0

FIGURE 6.—Interrelationship of genera and species of the family Gymnarthridae and *Saxonerpeton*. *pf* postfrontal, *po* postorbital. (1) Prefrontal: (1.0) far from external nares, (1.1) close to external nares, (1.2) reaching external nares. (2) Position of the jaw articulation: (2.0) close in front (less than 8% of skull length), (2.1) in front (between 10% and 14% of skull length), (2.2) far in front of occipital condyle-atlas articulation (24% of skull length). (3) Size of orbit: (3.0) very large (more than 25% of skull length), (3.1) large (20-25% of skull length), (3.2) medium (below 20% of skull length). (4) Size of external nares: (4.0) large, (4.1) very large, (4.2) medium. (5) Number of teeth on premaxillary: (5.5) 5, (5.4) 4, (5.3) 3. (6) Number of teeth on maxillary: (6.22) 22, (6.12) 12, (6.10) 10. (7) Number of small teeth behind enlarged teeth on the maxillary: (7.0) no enlarged teeth, (7.1) 4, (7.2) much enlarged teeth + 3 small behind (exception, type specimen of *E. primus*), (7.21) one tooth very much enlarged, (7.3) 2 small behind. (8) Retroarticular process: (8.0) absent, (8.1) present. (9) Shape of lacrimal at the anterior margin of the orbit: (9.0) only ventral process, (9.1) dorsal and ventral process, (9.11) deep dorsal process, (9.2) ventral process shortened. (10) Quadratojugal: (10.0) well separated from maxillary, behind jugal, (10.1) reaching below jugal, (10.11) reaching far rostrad below jugal and meeting maxillary. (11) Posterior margin of the skull table: (11.0) straight,

and Gaskill (1978) to *Cardiocephalus* and *Euryodus,* we have to assign only *sternbergi* to *Cardiocephalus,* and the other three species to *Euryodus.* The described specimen shows the characteristics of *Euryodus,* and must be assigned to *Euryodus* as a new species.

<div align="center">REVISED DIAGNOSES</div>

Cardiocephalus Broili, 1904

Small gymnarthrid microsaur with long, low skull. Jaw articulation far anterior to the occipital condyle-atlas articulation, posterior margin of the cheek region strongly inclined posteriorly. Long postorbital length (about twice the antorbital length). Small external nares with only the lacrimal on the posterior margin, prefrontal reaching rostrad half the distance between orbit and external naris. Medium sized orbits. High coronoid process on lower jaw. Stapes imperforate. Exoccipital not deeply notched to incorporate vagus foramen. Rows of teeth on pterygoid, vomer, ectopterygoid and palatine, but no palatal shagreen of denticles.

<div align="center">Type species and only species:
Cardiocephalus sternbergi Broili, 1904</div>

Euryodus Olson, 1939

Medium to large gymnarthrid microsaur. Skull elongated with widely rounded snout, jaw articulation anterior to occipital condyle-atlas articulation. Posterior margin of the cheek region straight or slightly inclined posteriorly. Large external nares, prefrontal reaching or nearly reaching the posterior margin of the external nares. Quadratojugal extending rostrad below the jugal. Stem of stapes perforate. Opening of vagus nerve penetrating exoccipital. Shagreen of teeth on the palate region, one row of teeth on ectopterygoid and palatine.

<div align="center">Type species: *Euryodus primus* Olson, 1939</div>

The type species *E. primus* is characterized by an enlarged single tooth on the maxillary below the orbit; *E. peabodyi* shows the same feature to a reduced extent (KU VP 8967). The occiput of *Euryodus primus* is slightly inclined forward in the dorsal part. Another characteristic feature of the species is the retroarticular

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(11.1) convex. (12) Posterior margin of the cheek region: (12.0) straight, (12.1) inclined backward, (12.11) inclined strongly backward, (12.2) straight and dorsally inclined forward. (13) Number of teeth on the margin of the lower jaw: (13.22) 22, (13.12) 12, (13.10) 10.

process. The species most closely related to *E. primus* is *E. peabodyi*. Both species have the most reduced number of premaxillary teeth (3) within the gymnarthrids. In both species, the quadratojugal reaches rostrad below the jugal or close to the maxillary. The lacrimal extends a dorsal process high up on the rostral margin of the orbit. *E. peabodyi* is smaller than *E. primus*, the orbit being larger, and the external nares smaller in proportion to the length of the orbit. Both species are easy to distinguish by the inclination of the posterior margin of the cheek region (*E. primus* straight and forward, *E. peabodyi* backward), and the posterior margin of the skull table (straight in *E. primus*, convex in *E. peabodyi*). Nearly as large as the type species is *E. dalyae*. The teeth are more rounded, blunter cones than in the other two species. The premaxillary bears five teeth as in *E. bonneri* and in more primitive gymnarthrids. The maxillary bears ten teeth like other species of *Euryodus* and *Cardiocephalus*. The prefrontal reaches the external nares, and the dorsal process of the lacrimal at the anterior margin of the orbit is shorter than in the two first species. The quadratojugal is low, and reaches just below the jugal. There are only ten teeth on the lower jaw as few as in *C. sternbergi* whereas the three other species of *Euryodus* have 12 or 13 teeth on the lower jaw. Characters in common in *E. dalyae* and *E. bonneri* are primitive characters within the genus and in themselves not conclusive enough to oppose both species to *E. peabodyi* and *E. primus*. The peculiarly shaped suture between tabular and postparietal on the occiput indicates a closer relationship of both species.

E. bonneri has a very narrow skull. The teeth are not blunt as in the other species; on the contrary, they are very pointed at least on the lower jaw. The prefrontal reaches the external naris broadly. The external nares are very large, with their length reaching half of the length of the very large orbit. Although the teeth are very different from the other three species of *Euryodus*, in all other features the described specimen differs only slightly from the other species.

The third Permian gymnarthrid genus from Texas, *Pariotichus*, is very difficult to separate from *Euryodus*, because the preservation of the skull is so poor. The prefrontal does not reach the external naris, but it comes as close as in the type specimen of *E. primus*. The lacrimal has a dorsal process on the anterior margin of the orbit as in *Euryodus*. There may be an elongated quadratojugal which could have reached the maxillary. The maxillary bears more teeth (12) than are usually found in *Euryodus* (10). It is difficult to decide how closely *P. brachyops* is related to *Euryodus* because of lack of sufficient information. It is left as a separate genus more closely related to *Euryodus*.

We argued above that the Permian European genus *Saxonerpe-*

ton may belong in the family Gymnarthridae. *Saxonerpeton* is a very small form, and like other small forms, it possesses a very large orbit compared to the length of the skull. *Saxonerpeton* is adapted to an aquatic life, in contrast to the tendency to terrestrial adaptation in Tuditanomorpha as indicated by the groove for a lateral line on the jugal of *Saxonerpeton* (Carroll and Gaskill, 1978: 38). The large mouth opening, peglike teeth, and the high number of teeth agree with this interpretation. These are primitive features within the Tuditanomorpha, and they distinguish the genus from all other genera within the family, but are not autapomorphies for the genus itself.

It is difficult to deal with the other Carboniferous genera (*Sparodus, Leiocephalikon,* and *Hylerpeton*) within the family because of scarcity of remains (Carroll and Gaskill, 1978: 72). The best known of the three genera is *Leiocephalikon.* The twelve teeth in the maxillary compare with *Pariotichus;* the twelve teeth in the lower jaw compare with three of the four *Euryodus* species. The number in *Hylerpeton* (15) and *Sparodus* (17) is higher. All other known features of *Leiocephalikon* are primitive within the Gymnarthridae. There exists a close resemblance in the sutures between the skull bones in *Leiocephalikon* and *Trachystegos.* The frontals have the same outline (compare Carroll and Gaskill, 1978, Fig. 46A with Carroll, 1966, Fig. 11A): an emargination on the lateral border, a posterolateral process of the right frontal, a posteromedial process of the left frontal in between the parietals, and a projection of the right frontal into the left. The suture between the parietals has the same course. The maxillary has a similar dorsal extension in front of the orbit in both specimens. But there is a distinct difference in size: *Trachystegos* is nearly three times as large as *Leiocephalikon.* This size difference explains the more exaggerated sculpture, the smaller pineal opening, and the larger, more blunt teeth in *Trachystegos.* There exists the possibility that *Trachystegos* is the adult form of *Leiocephalikon,* but further research is required. The differences could give us some indication about changes during ontogeny, assuming the interpretation is correct. For example, the number of teeth decreases from 12 in the lower jaw of *Leiocephalikon* to 10 in the lower jaw of *Trachystegos.*

In conclusion, *Euryodus* and *Cardiocephalus* can easily be distinguished, and their relationship can be settled. *Pariotichus* is close to *Euryodus.* The relationship of all the other genera of the Gymnarthridae (*Saxonerpeton,* and the Carboniferous genera) is not possible to define sufficiently because of lack of data.